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THESIS

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THE ELONGATION OF ROOT HAIRS AS AFFECTED BY LIGHT AND TEMPERATURE

R. E. JEFFS

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INTRODUCTION

The growth of higher plants involves not only cell-enlargement but cell-division and cell-differentiation as well. Cellular interaction may also be a modifying factor. The complexity of the phenomenon of growth is further increased by the fact that each of these phases in turn embraces several distinct processes. Cell-division involves on the one hand division of the plastids, vacuoles, and nuclei, with all the intricacies of mitosis, and on the other the formation of a partition. Cell-enlargement means not only extension of the cell wall and plasma membrane but deposition of new cell-wall material and the absorption of substances, especially foods, salts, and water, either by osmosis or by colloidal imbibition. Finally, cell-differentiation includes thickenings of the wall and changes in its chemical composition, the enlargement and fusion of the vacuoles, the formation of plastids, changes in the shape of the cell, and changes in the accumulation of storage substances, as pigments, foods, and alkaloids. Consequently, no single physical process like colloidal imbibition or hydration can be regarded as fully expressing the phenomenon of growth. It is to be noted that dry-weight increase, which has been frequently used as an index of growth, includes only certain of the processes of growth and also very much which is not growth at all, such as the effect of photosynthesis, respiration, transpiration, etc.

Environmental factors accelerating or retarding growth may accomplish this effect by accelerating or retarding all three phases or any one or two of them. For instance: The rate of increase in size of such a multicellular structure as a root or a stem may be retarded, either by lengthening the time required for cell-enlargement or by lengthening the time required for cell-division. This investigation is an attempt to throw some light upon the solution of this particular question.

Various instruments have been devised for measuring tissue-enlargement, from the simple auxanometer of Sachs (38) to the more complicated instruments of Pfeffer (35), MacDougal (31), Haines (18), Dowling (13), Bose (8), Jones (20), and others. The horizontal microscope has been used in the study of growth in both multicellular tissues and single cells. In the latter case it is necessary to depend almost entirely on this instrument, taking readings at frequent intervals by means of the eyepiece micrometer. It is

obvious that unicellular and filamentous forms of the algae and fungi, where the living cell can be easily isolated and elongation is comparatively rapid, lend themselves best to this method of investigation. Thus Blaauw (5), working on the growth of an individual cell, used the sporangiophore of *Phycomyces nitens*, and Miss Parr (34), in her investigations of the response of an organism to various kinds and intensities of light, has used the sporangiophore of Pilobolus. Noll (33) studied growth in Vaucheria, paying particular attention, however, to the method of wall-formation. It will be noted that in all three of these cases coenocytic forms have been used, the cells under consideration containing a large number of nuclei in a common cytoplasm. The condition in these cases then may be very different from that in which each nucleus is the center of a protoplast, as is the case in most cells, especially of the higher plants.

Very little if any work has been done on the rate of elongation of uninucleate cells of higher plants. A cell to be of value for this purpose must be readily visible with the compound microscope and should be free as far as possible from the influence of cell-division, cell-differentiation, and cellular interaction. That is, it should be a cell which is enlarging but which will not again divide, the differentiation should be very slight, and the cell should be little affected by pressure and tension of neighboring cells. Only a few cells of this kind are to be found in the complex system of tissues such as one finds in the higher plants. Trichomes, pollen tubes, and root hairs are among the few which conform to these requirements. Of these the last named was chosen for this study. In this structure cell-division is completed before the hair begins to form. Although new wall material is doubtless being deposited very rapidly during the growth of the root hair, this is more a matter of cell-enlargement than a case of differentiation, as the term is ordinarily used in relation to cell-growth. Finally, the elongating root hair, as will be shown later, is only for a time directly affected by cellular interaction.

Investigations made on root hairs have been confined to the composition of their walls, the cause of their formation, and the conditions under which they may form or by which their formation may be inhibited. Thus the work of Schwarz (40), Devaux (12), Leavitt (25), Miss Roberts (36), Miss Bardell (3), Miss Snow (44), and others, include investigations on the effect of temperature, transpiration, light, moisture, contact, wounding, mechanical retardation, length of cell, food supply, and oxygen on the initiation or inhibition of root-hair formation. Very little if any work has been done from the standpoint of the normal rate of growth or of the effect of the environmental factors upon the rate of growth.

Methods and Scope of Investigation

The pop corn (*Zea mays* L., sub-species *everta* Sturt.), the common garden radish (*Raphanus sativus* L.), and the white mustard (*Sinapis alba* L.)' were

selected for this study. Two different schemes of germination were employed. The seeds were first germinated on gauze stretched over glass jars partly filled with water. This resulted in the roots being straight but very slender, and it was later found preferable to germinate the seeds on damp filter paper, laid upon a plate of glass and covered with a bell jar to keep them moist. The whole was kept in the dark at room temperature. By this method more stocky seedlings with a better development of root hairs were secured. Germination began in the case of the radish in about 36 hours, and 12 hours later the roots were of sufficient length to be transferred to the moist chamber described below. The corn was somewhat slower in both germination and growth, about 48 hours elapsing before the pericarp burst.

The moist chambers were a modification of the type used by Blaauw (7) in his work on the growth and phototropism of roots. They were made by using pairs of glass plates, in size 5 x 7.5 cm. These two plates were separated by several thicknesses of filter paper from which two oval sections had previously been cut, leaving the filter paper in the form of a frame. Narrow openings (about 3 cm. wide) were cut at the top, through which the roots of the seedlings were passed. The chambers were bound at the ends with strong linen thread. The filter paper was then saturated with water and the seedlings were inserted (fig. 1, Plate LXII).

The chambers containing seedlings were placed upright inside a large crystallizing dish, covered with a glass, and placed in a dark constant-temperature room. During the earlier trials a thin layer of water was placed in the dish in which the chambers stood. This resulted in moisture condensing on the inner walls of the chambers, which was found to be unsatisfactory because the root hairs so grown were constantly swelling at the tip and bursting, making them useless for study. Miss Roberts (36) found in her investigations that, if moisture was reduced sufficiently, there was a lack of root-hair development or they failed to elongate. She considers that this reduction in moisture content has a direct effect upon the walls, making them less elastic and not so easily extended. It appears then that there is an optimum humidity for root-hair development, below which they do not appear at all and above which they burst. If Miss Roberts' contention is correct, it may be that in a saturated atmosphere the colloidal root-hair wall may be softened by imbibition and be easily stretched to the bursting point under the existing conditions of osmotic pressure maintained in the root hair. It was then found that the proper humidity could be attained by moistening several thicknesses of filter paper and placing them in the bottom of the dish after most of the free water had been removed. The chambers stood erect upon this, and when covered the large container required no addition of moisture for a week or more. Under these conditions, trouble from bursting hairs was nearly eliminated and excellent root-hair development took place. After standing in the constant-temperature room over night, the seedlings were in good condition for use.

The investigations were carried on in a basement room having thick cement walls and no windows. The temperature of this room did not vary more than three degrees during the entire time of experimentation. During the course of any one set of observations covering from three to ten hours, the temperature of the room seldom varied more than one half of one degree. Except in experiments on the effect of light, the only illumination permitted was a red light of low candle power which was turned on only while making the adjustment of the moist chamber on the microscope, and in taking readings. The microscope tube was shifted to the horizontal position so that the moist chamber could be placed on the stage in a vertical position. The mirror was so arranged that the light from the red lamp, placed at some distance at one side, would be reflected in the field of the microscope. A special eyepiece micrometer was used, with an adjusting screw which enabled one to move the micrometer scale across the field of vision at right angles to the length of the scale. This permitted keeping the scale over the root hair during the early part of its growth, when lateral (downward) movement was conspicuous, without moving the moist chamber on the stage.

Measurements were taken of the root hairs every fifteen minutes at first. Later, with a higher-power objective, five- and ten-minute intervals were used. Measurements were begun at the time the root hair appeared as a slight protuberance on the root, and a root hair was always chosen which from its location would be likely to grow at right angles to the axis of the microscope.

The Grand Period of Elongation of Root Hairs

The primary purpose in studying the grand period of growth of root hairs under constant conditions in connection with this investigation was to determine if there is an interval during which elongation is comparatively uniform. If such a period of time exists, then the hair becomes a satisfactory subject for the study of the effect of external factors, such as light and temperature, on the enlargement of the cell.

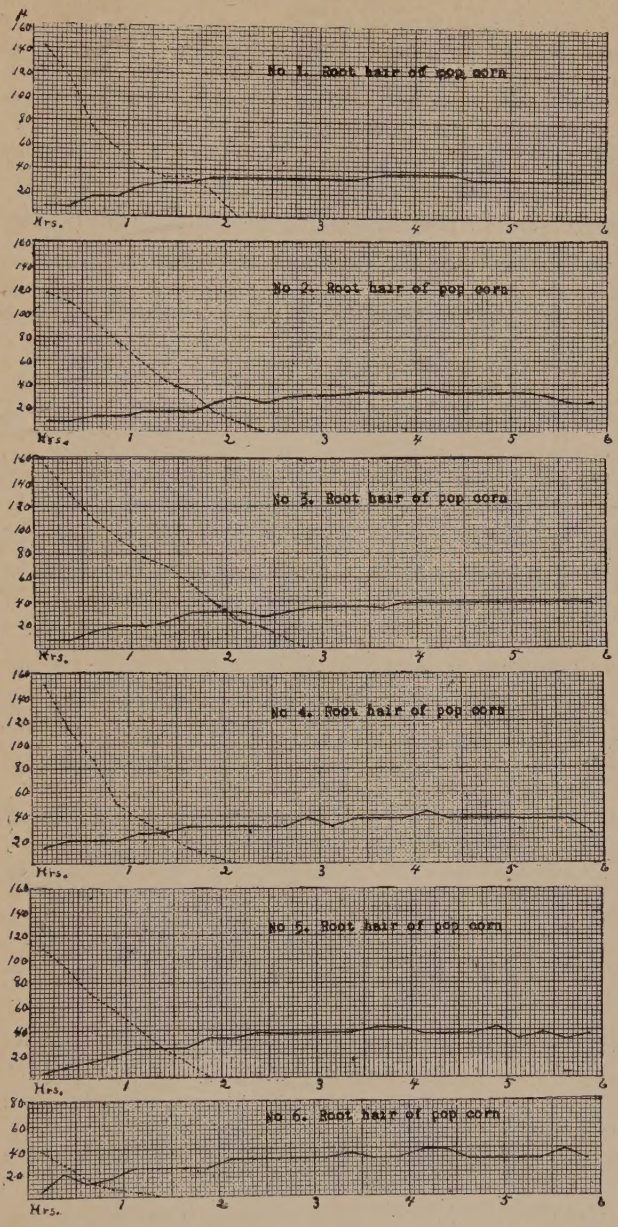
The lists of readings numbered 1–18 below, and graphs 1–18 (text figs. 1, 2) present the results obtained from the following studies.

(*a*) Six root hairs of pop corn were measured as to root-hair elongation and lateral movement, readings being taken at 15-minute intervals for six hours, with a view to studying the beginning of the grand period of growth. The temperatures were 23° C. in nos. 1, 2, and 5, and 22° C. in nos. 3, 4, and 6.

Root-hair elongation in microns per 15-minute interval was as follows:

No. 1. 8.3; 8.3; 16.7; 16.7; 25.0; 29.2; 29.2; 33.4; 33.4; 33.4; 33.4; 33.4; 33.4; 33.4; 37.5; 37.5; 37.5; 37.5; 33.4; 33.4; 33.4; 33.4; 33.4; 33.4.

No. 2. 8.3; 8.3; 12.5; 12.5; 16.7; 16.7; 16.7; 25.0; 29.2; 25.0; 29.2; 31.3; 31.3; 33.4; 33.4; 33.4; 37.5; 33.4; 33.4; 33.4; 33.4; 31.3; 25.0; 25.0.


No 1. Root hair of pop corn
No 2. Root hair of pop corn
No 3. Root hair of pop corn
No 4. Root hair of pop corn
No 5. Root hair of pop corn
No 6. Root hair of pop corn
Hrs.

TEXT FIG. 1. Six root hairs of pop corn at the beginning of the grand period of growth, showing the relation between root-hair elongation and lateral movement of the entire hair. The solid line gives the root-hair elongation, the broken line lateral movement. Readings taken at 15-minute intervals.

No. 3. 7.7; 7.7; 15.4; 19.3; 19.3; 23.1; 30.8; 30.8; 30.8; 27.0; 30.8; 34.7; 34.7; 34.7; 34.7; 38.5; 38.5; 38.5; 38.5; 38.5; 38.5; 38.5; 38.5; 38.5.

No. 4. 12.5; 18.7; 18.7; 18.7; 25.0; 25.0; 31.2; 31.2; 31.2; 31.2; 31.2; 37.5; 31.2; 37.5; 37.5; 37.5; 43.7; 37.5; 37.5; 37.5; 37.5; 37.5; 37.5; 37.5; 25.0.

No. 5. 4.1; 8.3; 12.5; 16.7; 25.0; 25.0; 25.0; 33.4; 33.4; 37.5; 37.5; 37.5; 37.5; 37.5; 41.7; 41.7; 37.5; 37.5; 37.5; 41.7; 33.4; 37.5; 33.4; 37.5.

No. 6. 3.9; 19.3; 11.6; 15.4; 23.1; 23.1; 23.1; 23.1; 30.8; 30.8; 30.8; 30.8; 30.8; 34.7; 30.8; 30.8; 38.5; 38.5; 30.8; 30.8; 30.8; 30.8; 38.5; 30.8.

Lateral movement in microns per 15-minute interval was as follows:

No. 1. 141.9; 116.9; 75.1; 58.4; 41.7; 33.4; 33.4; 20.8; 00.0 (no lateral movement after 2 hours).

No. 2. 116.9; 108.5; 91.8; 75.1; 58.4; 41.7; 33.4; 16.5; 8.3; 0.0 (no lateral movement after $2\frac{1}{4}$ hours).

No. 3. 154.0; 130.9; 107.8; 92.4; 77.0; 69.3; 53.9; 38.5; 23.1; 19.3; 7.7; 0.0 (no lateral movement after $2\frac{3}{4}$ hours).

No. 4. 150.0; 112.5; 87.5; 50.0; 37.5; 25.0; 12.5; 6.2; 0.0 (no lateral movement after 2 hours).

No. 5. 108.5; 91.8; 75.1; 58.4; 41.7; 25.0; 12.5; 00.0 (no lateral movement after $1\frac{3}{4}$ hours).

No. 6. 38.5; 27.0; 11.6; 7.7; 3.9; 0.0 (no lateral movement after $1\frac{1}{4}$ hours).

(*b*) Six root hairs of radish were measured as to root-hair elongation and lateral movement, readings being taken at 15-minute intervals for from $5\frac{1}{2}$ to 6 hours. The temperatures were 23°–23.5° C. in no. 7, 23.5°–24° C. in nos. 8 and 9, 22.5° C. in no. 10, and 24.5° C. in nos. 11 and 12.

Root-hair elongation in microns per 15-minute interval was as follows:

No. 7. 20.8; 25.0; 29.2; 29.2; 37.5; 37.5; 33.4; 33.4; 33.4; 33.4; 29.2; 33.4; 25.0; 33.4; 29.2; 29.2; 33.4; 33.4; 33.4; 33.4; 33.4; 33.4.

No. 8. 6.2; 6.2; 12.5; 25.0; 31.2; 37.5; 37.5; 43.7; 37.5; 31.2; 37.5; 37.5; 37.5; 37.5; 37.5; 37.5; 37.5; 37.5; 43.7; 43.7; 37.5; 50.0; 43.7; 43.7; 50.0.

No. 9. 23.1; 23.1; 30.8; 46.2; 46.2; 38.5; 38.5; 46.2; 46.2; 46.2; 46.2; 50.0; 50.0; 46.2; 46.2; 53.9; 53.9; 46.2; 53.9; 46.2; 46.2; 46.2; 46.2; 46.2.

No. 10. 8.3; 8.3; 8.3; 16.7; 25.0; 16.7; 16.7; 29.2; 25.0; 29.2; 29.2; 29.2; 37.5; 33.4; 33.4; 41.7; 45.9; 50.1; 50.1; 50.1; 50.1; 50.1; 50.1; 50.1.

No. 11. 12.5; 12.5; 22.0; 15.6; 25.0; 18.7; 31.2; 31.2; 43.7; 41.6; 46.8; 43.7; 43.7; 50.0; 43.7; 43.7; 50.0; 50.0; 37.5; 50.0; 50.0; 50.0; 50.0.

No. 12. 12.5; 18.7; 25.0; 25.0; 31.2; 37.5; 37.5; 43.7; 43.7; 46.8; 46.8; 43.7; 50.0; 43.7; 43.7; 43.7; 50.0; 50.0; 50.0; 56.2; 50.0; 43.7.

Lateral movement in microns per 15-minute interval was as follows:

No. 7. 50.1; 25.0; 8.3; 0.0 (no lateral movement after 45 minutes).

No. 8. 100.0; 87.5; 62.5; 50.0; 25.0; 12.5; 00.0 (no lateral movement after $1\frac{1}{2}$ hours).

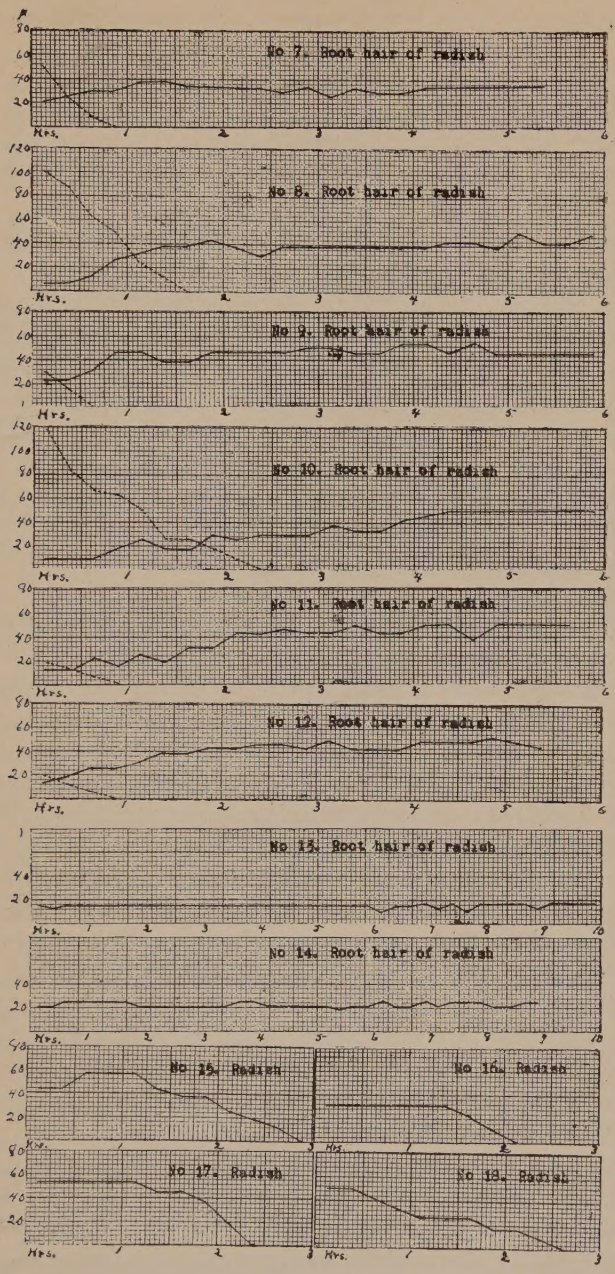
No. 9. 30.8; 15.4; 00.0 (no lateral movement after 30 minutes).

No. 10. 116.9; 83.5; 66.8; 62.6; 50.1; 25.0; 25.0; 16.7; 8.3; 0.0 (no lateral movement after $2\frac{1}{4}$ hours).

No. 11. 18.7; 12.5; 6.2; 0.0 (no lateral movement after 45 minutes).

No. 12. 18.7; 12.5; 6.2; 0.0 (no lateral movement after 45 minutes).

(*c*) Two root hairs of radish were measured as to rate of root-hair elongation after lateral movement had ceased, readings being taken at 15-minute intervals for 10 and 9 hours respectively. The temperature was 23° C. in no. 13 and 24° C. in no. 14.


No 7. Root hair of radish
No 8. Root hair of radish
No 9. Root hair of radish
No 10. Root hair of radish
No 11. Root hair of radish
No 12. Root hair of radish
No 13. Root hair of radish
No 14. Root hair of radish
No 15. Radish
No 16. Radish
No 17. Radish
No 18. Radish
Hrs.

TEXT FIG. 2. Nos. 7–12 show the relation between root-hair elongation and lateral movement in six radish root hairs at the beginning of the grand period. Nos. 13 and 14 show the rate of elongation of two radish root hairs, studied for 10 and 9 hours respectively, after lateral movement had ceased. Nos. 15–18 show the rate of elongation of four radish root hairs at the close of the grand period of growth. Readings at 15-minute intervals in all cases.

Root-hair elongation in microns per 15-minute interval was as follows:

No. 13. 29.2; 25.0; 29.2; 20.8; 29.2; 29.2; 33.4; 25.0; 29.2; 20.8; 29.2; 29.2; 29.2; 29.2; 25.0; 29.2; 29.2; 29.2; 29.2.

No. 14. 43.7; 43.7; 50.0; 50.0; 50.0; 50.0; 50.0; 43.7; 43.7; 43.7; 43.7; 43.7; 43.7; 43.7; 50.0; 50.0; 43.7; 43.7; 43.7; 43.7; 43.7; 37.5; 43.7; 43.7; 50.0; 43.7; 43.7; 50.0; 43.7; 50.0; 50.0; 50.0; 43.7; 43.7; 50.0; 50.0.

(*d*) Four root hairs of radish were measured as to root-hair elongation, readings being taken at 15-minute intervals, with a view to studying the close of the grand period of growth. Root hairs were chosen whose length indicated that they were approaching the close of the grand period. The temperatures were 23.5° C. in no. 15, 23° C. in no. 16, and 24° C. in nos. 17 and 18.

Root-hair elongation in microns per 15-minute interval was as follows:

No. 15. 43.7; 43.7; 56.2; 56.2; 56.2; 43.7; 37.5; 37.5; 25.0; 18.7; 12.5; 0.0.
No. 16. 30.8; 30.8; 30.8; 30.8; 30.8; 30.8; 23.1; 11.5; 0.0.
No. 17. 53.9; 53.9; 53.9; 53.9; 53.9; 46.2; 46.2; 38.5; 19.2; 0.0.
No. 18. 50.1; 50.1; 41.7; 33.4; 25.0; 25.0; 25.0; 16.7; 16.7; 8.3; 0.0.

It is evident from these observations that:

1. The grand curve of elongation of the root hair resembles the grand curve for growth in general.

Elongation here begins slowly, increasing in rate for an average of 1½ to 2 hours. It then becomes constant with only minor variations for a number of hours (9 to 10 hours are shown in nos. 13 and 14), and then falls to zero. This resembles the results obtained by Sachs (39) on the rate of growth of the whole root under fairly uniform conditions. Working with the root of *Vicia faba*, the temperature varying between 18° and 24.5° C. each day, he got the following results, readings being taken in 24-hour periods: 1.8 mm.; 3.7; 17.5; 16.5; 17.0; 14.5; 7.0; 0.0. These results show a much flattened curve as do those with root hairs, growth increasing up to the third day, then remaining fairly constant for three days when it begins to decrease, falling to zero on the eighth day. The grand period of growth of root hairs is thus found to correspond to that of multicellular tissues.

2. There is a definite relation between root-hair elongation and lateral movement, elongation being gradually accelerated as lateral movement is retarded. (See figs. 7–9, Pl. LXII.)

Root hairs as they make their appearance are for a time carried along laterally, that is, parallel to the axis of the root. This lateral movement is due to the overlapping of the lower part of the zone of root-hair formation and the upper part of the zone of the root in which cell-elongation occurs.

Concerning the cause of the initial swelling in hair-formation, Miss Snow (44) found that the average vertical length of epidermal cells which produce root hairs is less than of those which do not produce root hairs in the same root. Miss Bardell (3) found the same to be true. This fact would indicate

that there may be a relationship between the inability of the cell to elongate vertically and the development of lateral protrusions, namely, root hairs. Indeed, cellular interaction may very probably be an important factor. Miss Snow (44) found in corn roots grown in water, bearing no root hairs, that both epidermal and cortical cells are greatly elongated, while in roots grown in air, bearing root hairs, the cells become shorter and thicker toward the central cylinder. She found experimentally that retarding the vertical elongation of roots, by growing them in small glass tubes closed at the base, resulted in increased production. From this she developed the theory that the retarding effect of the subepidermal cells of the cortex on those of the epidermis initiates root-hair formation. Miss Snow's theory is strongly supported by my data. The root hairs appear on the roots of the pop corn and radish where vertical cell-elongation is being checked, as shown by the decrease in the rate at which the root elongates at this point. Thus the subepidermal cells, checking vertical cell-elongation in the epidermis, bring about the formation of lateral evaginations which later develop into root hairs, an excellent example of cellular interaction.

It is possible also to see how the gradual decrease in vertical elongation of the epidermal cells may account for the gradual increase in the rate of root-hair elongation. A retardation in the rate of vertical elongation of the cells of the root is doubtless accompanied by a gradual increase in the osmotic pressure. If the osmotic pressure continues to increase at the same rate as vertical elongation is retarded, the osmotic pressure of the cells will increase enormously. Now, in the subepidermal cells of the cortex this increased pressure would be equalized by the pressure of the adjoining cells on opposite sides of the walls between them. The same would be true of the lateral and inner walls of the epidermis. Miss Roberts (36) found a pressure equivalent to five atmospheres in the epidermal cells which she studied. This means that the outer wall of the epidermal cell is under strong pressure from within, five times as great as that on the outside. As the pressure here becomes gradually greater, the outer wall tends to push out. If a portion of this wall is weaker than the rest, it would be extended, forming a narrow protuberance. Such may be the explanation of the first appearance of the root hair. Its rate of growth should gradually increase as the pressure in the cell increases. When lateral movement has ceased, usually within two to three hours or less in the roots studied, then the internal pressure in the cell becomes stabilized and elongation of the root hair continues, if kept under uniform conditions, with only minor variations in its rate of growth.

There is some difference as regards the length of time lateral movement continues in the case of different root hairs. Thus for the corn the shortest time was $1\frac{1}{2}$ hours and the longest 3 hours, with an average time of $2\frac{1}{5}$ hours. The average time for the six radish roots was $1\frac{1}{3}$ hours with a greater range of variation, being from $\frac{3}{4}$ of an hour to $2\frac{1}{2}$ hours.

3. The rate of elongation of root hairs on any one root is quite uniform.

From observations made during these investigations it would appear that the slight differences in length of root hairs in any one region of the root are due more to the age of the root hairs, that is, to the relative time of initiation, than to their rate of growth. The different lengths of root hairs found at about the same level, shown in the photograph of a radish root (fig. 4, Pl. LXII), are due to differences in age rather than to differences in rate of elongation. Sometimes one or more root hairs will develop for some time before others start in their vicinity. This gives an irregularity in length which might be thought due to a difference in the growth rate.

4. Of the two species studied, the root hairs grew more slowly on the one in which they were produced in greatest abundance.

A much larger proportion (three or four times as many) of the epidermal cells of the corn produced root hairs than did those of the radish (compare figs. 5 and 6, Pl. LXII). After lateral movement ceased, the radish root hairs studied grew at a rate varying for the most part from 31 to 50 microns per 15-minute interval, with an average rate of 41 microns. The rate of root-hair growth in the corn under the same conditions varied from 29 to 38 microns per 15-minute interval, with an average rate of 35 microns. This shows that the radish root hairs, which comparatively speaking are scattered, grow more rapidly than do those of the corn.

The Effect of Light on the Rate of Root-hair Elongation

The effect of light on the direction and rate of growth of plant parts has been studied by Sachs (38), Duchartre (14), Hofmeister (19), Pfeffer (35), and others. The facts that internodes of stems often grow more rapidly in the dark than when exposed to light, and that shoots tend to bend toward the source of a one-sided illumination, have been taken as proof that light has a retarding effect upon growth. Exceptions to this are found, however, as in the case of leaves, tendrils, and certain internodes, which elongate more on the side exposed to light.

It is within the last fifteen years that the most careful work on the effect of light on growth has been carried on. Much of this has been a study of phototropic bending in multicellular organs. The coleoptiles of cereals, particularly of *Avena sativa*, have been used extensively in these investigations because of their great sensitivity to the light stimulus. Clark (10), Arisz (1), Vogt (48), Sierp (42), Brauner (9), and others have shown a positive bending of this structure under the influence of light, indicating that light retards growth.

Other plant parts used have been the hypocotyls and roots of various seedlings. Blaauw (6) worked with the hypocotyl of the sunflower (*Helianthus globosus*) and obtained, on the whole, a retardation of growth in the light. His results with the roots of *Lepidium sativum*, *Avena sativa*, *Raphanus sativus*, and *Sinapis alba* were not so consistent. Lighting with 130,000

M. C. S., which produced a strong reaction of the Helianthus hypocotyl, led to a scarcely measurable retardation in the Lepidium root. With *Avena sativa* he got even less evidence of a retardation. This seemed to him rather surprising inasmuch as the coleoptile of this plant is so extremely sensitive to light. He then tested *Raphanus sativus* and says that the root of this plant is so insensitive to light that even with a lighting of 2000 M. C. during four hours it showed no light-growth reaction and continued to grow as in the dark. Lastly he used the root of *Sinapis alba* and obtained a light-growth reaction, quite strongly developed in 1500 M. C. and clearly evident in 64 M. C., but weak and questionable in 8 M. C. The decrease in growth rate in the *Sinapis alba* root in 1500 M. C. was about the same as in the Helianthus hypocotyl in one M. C. Blaauw then estimates the sensitivity of the Helianthus hypocotyl to be at least one thousand times that of the root of white mustard.

Such studies as these, while very important in the study of the effect of light upon complex tissue systems, contribute only slightly to the question of the effect of light on cell processes. Variation in the growth rate must be primarily produced by cellular changes. A decrease in the rate of elongation of a multicellular tissue may be the result of a longer time required for the cells to enlarge, or it may be due to a longer time required for cell-division to take place. The following investigations have been carried on in order to determine if the effect of light in retarding the rate of growth in the higher plants is an effect on cell-enlargement or on cell-division.

Previous work of this nature has been confined to the lower plants, particularly the *Mucorales*. Lendner (28) noted that the sporophores of many members of this group become elongated in the dark, light having a retarding effect on their development. Probably the most important work of this kind is that of Blaauw (5) on the sporophores of *Phycomyces nitens*. Blaauw got on the whole an acceleration in growth in 1- and 64-meter candle power, while in higher intensities (4000 M. C.) a retardation was noted. It is to be remembered that these *Mucorales* are all coenocytic and thus differ from the uninucleate root hairs. It may even be that the effect of light in retarding enlargement of these hyphae is an effect on nuclear division rather than on the process of cell-enlargement *per se*.

The work already done on light in its relation to root hairs has been confined to a study of its effect on their abundance. Schwarz (40) found that light had no effect on hair-production in *Zea mays* and *Pisum sativum*. Devaux (12) found that light retarded elongation of the cells of the root of *Zea mays* and favored hair-production. Miss Snow (44), working with *Triticum vulgare*, *Pisum sativum*, and *Cucurbita Pepo*, reached the conclusion that light or darkness has little effect on root-hair production, and any slight effect found she considered due to an indirect effect upon growth.

Root-hairs of *Raphanus sativus* L. and *Sinapis alba* L. were used in this study. These were grown as described above for the investigations on the

grand period of growth, the work being carried on in a constant-temperature room. The light was obtained from (Mazda) gas-filled frosted bulbs, with the exception of the strongest illumination which was obtained from a large clear bulb made for use in projecting lanterns. The lamps were carefully calibrated, so their exact candle power was known. The bulb was placed in a projecting lantern and the horizontal microscope placed before it at a given distance, so that the light, when turned on, fell directly upon the root mounted on the stage. A thermometer was placed beside the mount in order that any change in temperature might be noted.

In each case a root hair was chosen, the lateral movement of which had ceased, and which therefore was practically constant in its growth rate in the dark. The rate of growth was recorded for an hour before the light was applied, in order to be sure that growth in the dark was uniform. Readings were taken at from 5- to 10-minute intervals, the light being turned on during one period except when continuous lighting was used. The distance between light and object was carefully measured.

Lists numbered 19–30 below, and graphs 19–30 (text fig. 3) present the results obtained from a study of 12 root hairs of radish (*Raphanus sativus* L.).

No. 19. Interval 5 min. Temp. 15.5° C. Illumination 15720 M. C. S.: 10.5; 10.5; 7.0; 7.0; 7.0; 10.5; 10.5; 10.5; 7.0; 8.7; (Light 10.5); 10.5; 10.5; 14.0; 10.5; 10.5; 14.0; 10.5; 10.5; 10.5; 10.5; 10.5; 14.0; 10.5; 7.0.

No. 20. Interval 5 min. Temp. 16° C. Illumination 15720 M. C. S.: 14.0; 14.0; 14.0; 12.3; 12.3; 14.0; 5.3; 12.3; 12.3; 10.5; 14.0; 19.3; 14.0; (Light 14.0); 12.3; 14.0; 14.0; 8.8; 12.3; 12.3; 10.5; 10.5; 10.5; 14.0; 10.5; 8.8; 10.5; 10.5; 10.5; 12.3.

No. 21. Interval 5 min. Temp. 16°–16.5° C. Illumination 15720 M. C. S.: 3.5; 3.5; 5.3; 5.3; 5.3; 5.3; 5.3; 5.3; 5.3; 5.3; (Light 3.5); 5.3; 5.3; 5.3; 5.3; 7.0; 7.0; 5.3; 7.0; 7.0; 7.0; 5.3; 7.0; 5.3; 8.8; 22.8; 7.0; 7.0; 5.3; 7.0; 7.0; 5.3.

No. 22. Interval 10 min. Temp. 17.5° C. Illumination 125760 M. C. S.: 14.0; 14.0; 14.0; 14.0; 17.5; 14.0; (Light 10.5); 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 10.5; 10.5; 14.0; 14.0; 10.5; 14.0.

No. 23. Interval 10 min. Temp. 13.5° C. Illumination 125760 M. C. S.: 14.0; 10.5; 14.0; 14.0; 14.0; 14.0; 12.3; 14.0; (Light 14.0); 14.0; 14.0; 14.0; 14.0; 14.0; 17.5; 14.0; 14.0; 14.0; 14.0; 10.5; 14.0; 17.5; 14.0; 10.5.

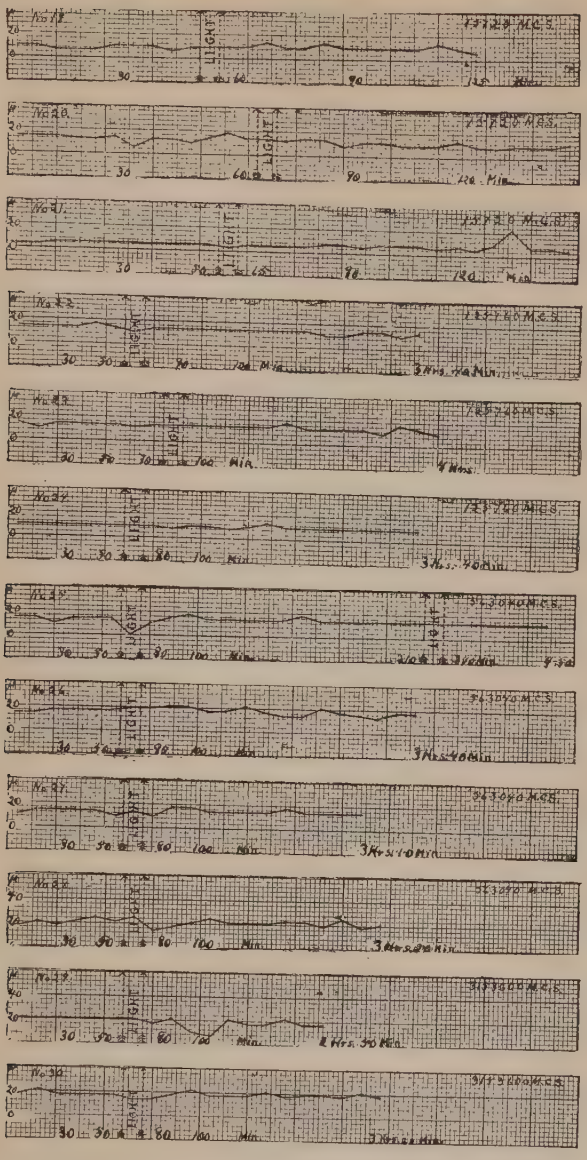
No. 24. Interval 10 min. Temp. 14° C. Illumination 125760 M. C. S.: 10.5; 10.5; 10.5; 10.5; 10.5; 10.5; (Light 10.5); 10.5; 8.8; 10.5; 10.5; 8.8; 10.5; 14.0; 10.5; 10.5; 10.5; 10.5; 10.5; 10.5; 10.5; 10.5; 10.5.

No. 25. Interval 10 min. Temp. 14.5° C. Illumination 563040 M. C. S.: 14.0; 14.0; 10.5; 14.0; 14.0; 14.0; (Light 00.0); 10.5; 14.5; 17.5; 14.0; 14.0; 14.0; 14.0; 14.0; 17.5; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; (Light 14.0); 14.0; 14.0; 14.0; 14.0; 14.0; 4 .0.

No. 26. Interval 10 min. Temp. 16° C. Illumination 563040 M. C. S.: 14.0; 14.0; 17.5; 17.5; 17.5; 17.5; (Light 19.3); 19.3; 21.0; 21.0; 17.5; 17.5; 21.0; 17.5; 14.0; 14.0; 21.0; 17.5; 15.8; 12.3; 17.5; 17.5.

No. 27. Interval 10 min. Temp. 16° C. Illumination 563040 M. C. S.: 10.5; 14.0; 14.0; 14.0; 14.0; 10.5; (Light 14.0); 10.5; 17.5; 17.5; 14.0; 14.0; 14.0; 14.0; 17.5; 14.0; 14.0; 14.0; 14.0.

No. 28. Interval 10 min. Temp. 16°–17.5° C. Illumination 563040 M. C. S.: 17.5; 21.0; 17.5; 21.0; 24.5; 21.0; (Light 24.5); 14.0; 17.5; 21.0; 24.5; 21.0; 21.0; 21.0; 22.8; 22.8; 19.3; 24.5; 17.5; 21.0.



TEXT FIG. 3. Graphs showing the result of the application of light to twelve root hairs of radish, illumination varying from 15720 M. C. S. to 3153600 M. C. S. For discussion see text.

No. 29. Interval 10 min. Temp. 19.5°–22° C. Illumination 3153600 M. C. S.: 21.0; 21.0; 21.0; 21.0; 21.0; 21.0; (Light 21.0); 17.5; 21.0; 10.5; 7.0; 21.0; 17.5; 17.5; 21.0; 17.5; 17.5.

No. 30. Interval 10 min. Temp. 16°–19° C. Illumination 3153600 M. C. S.: 17.5; 21.0; 17.5; 17.5; 17.5; 17.5; (Light 14.0); 14.0; 17.5; 21.0; 17.5; 17.5; 17.5; 21.0; 17.5; 19.3; 19.3; 17.5; 21.0; 17.5.

An examination of no. 19, with a lighting of 15720 M. C. S., shows no retardation but instead a slight acceleration at three points. This acceleration is noted during one 5-minute interval, the rate returning to normal during the following 5 minutes. These variations are no greater than those noted in root hairs grown in the dark (nos. 1–14).

No. 20 presents the growth of a root hair showing more variation in the growth rate than does no. 19. Two minima occurred after exposure, but these can not be considered a light effect, for a retardation of even greater amount is noted before the root was illuminated.

The root hair represented by no. 21 has a quite uniform growth except for a 10-minute interval about 1¼ hours after light was applied. During this time growth was greatly accelerated for 5 minutes, returning to normal during the next 5 minutes. Because of the time which has elapsed since lighting, and because of the fact that no corresponding acceleration occurs in the other root hairs growing under the same illumination, this variation can not be considered as being due to light. Similar sudden variations in the growth rate, lasting for from 10 to 15 minutes, have been noted by the writer in root hairs growing in continuous darkness.

Nos. 22, 23, and 24, illumination 125760 M. C. S., show great uniformity in growth rate both before and after lighting. No. 22 shows a slight retardation during the lighting period and another slight retardation for about 20 minutes, over 1½ hours later. No. 24 shows two 10-minute periods of slight retardation, one 10 minutes after lighting and another 20 minutes later. On the whole, the slight variations are no more than might be expected were light not applied.

No. 25, illumination 563040 M. C. S., shows a complete cessation of growth in length after light is applied. However, this growth is resumed in the dark and returns to the normal rate inside of 20 minutes. During this interval of suspended elongation the root hair swelled at the tip, so that growth continued as an increase in diameter rather than in length. That this stoppage in elongation is due to the effect of light is questionable. The swelling at the tip would indicate a temperature effect, as shown in later studies. However, no rise in temperature was noted here. It is seen that the light when applied 2½ hours later to the same root hair for the same period of time produced no variation in its growth rate.

No. 26, with the same illumination as no. 25, shows an acceleration of growth following exposure to light. This is followed nearly 1½ hours later by a retardation amounting to 7 microns per interval, within 20 minutes. This retardation lasts through two 10-minute intervals. However, the rate here is no slower than that observed during the first two periods in darkness, so that it can not be considered of any significance.

No. 28 shows some irregularities in growth both before and after lighting. The rate in darkness varies from 17 to 24 microns per 10-minute interval, and the same variations are found after lighting except in the period immediately following, when the growth is but 14 microns.

In the studies under strong lighting the temperature factor was not entirely eliminated. A thermometer standing just in front of the moist chamber showed an increase in temperature of from $2\frac{1}{2}$ to 3 degrees C., during the 10-minute interval that light was applied. In most cases a swelling of the tip occurred (fig. 3, Pl. LXII). During this interval of swelling, growth in length was greatly retarded. It is entirely likely that this swelling was due not to the effect of strong light but to increase in temperature, which will be shown later to have a marked effect on root-hair growth.

In no. 29, illumination 3153600 M. C. S., we find a decided retardation, with swelling of the tip, coming about 40 minutes after lighting. It is questionable whether this is the result of lighting, change of temperature, or some other unknown cause. Such peculiarities in the growth rate do occasionally occur in root hairs grown in the dark under uniform conditions of temperature and moisture.

No. 30, illumination as before, shows a slight retardation during the application of light and during the 10-minute interval following. This retardation was accompanied by some swelling of the tip. Following this, growth was much the same as before illumination.

It appears then that *the root hairs of Raphanus sativus, under light intensities ranging from 15720 M. C. S. to 563040 M. C. S., show no light-growth reaction.* It is also likely that much brighter illumination (3153600 M. C. S.) has no effect. Variations which do occur after lighting come at no uniform intervals and are no greater than when the root hairs are grown continuously in the dark.

Finding apparently no reaction to light in the root hair of *Raphanus sativus*, *Sinapis alba* was next investigated. The root of this plant, being the one in which Blaauw (7) obtained positive evidences of retardation in growth, would seemingly be the most satisfactory of any known for this purpose. Here four light intensities of short duration and one series under continuous lighting were used. Lists numbered 31–44 and graphs 31–44 (text fig. 4) show the results of these experiments.

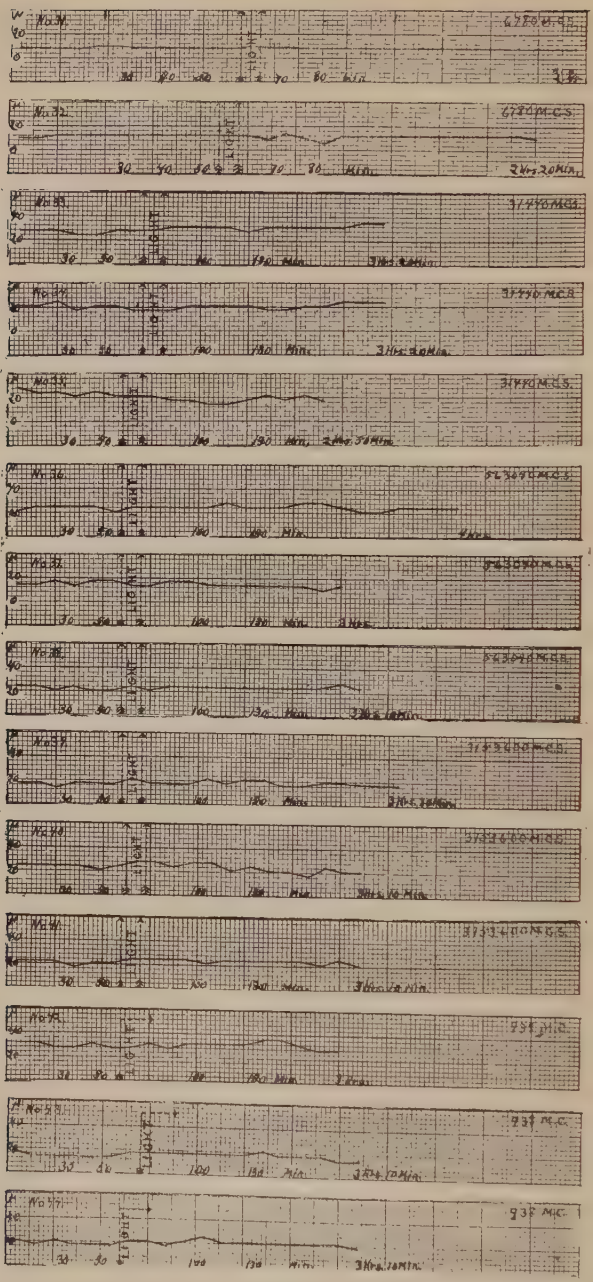
No. 31. Interval 5 min. Temp. 16° C. Illumination 6780 M. C. S.: 8.8; 8.8; 8.8; 8.8; 10.5; 10.5; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; (Light 10.5); 9.7; 9.7; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8; 8.8.

No. 32. Interval 5 min. Temp. 20° C. Illumination 6780 M. C. S.: 10.5; 10.5; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; (Light 12.3); 12.3; 9.8; 14.0; 10.5; 5.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 12.3; 10.5.

No. 33. Interval 10 min. Temp. 18° C. Illumination 31440 M. C. S.: 28.0; 28.0; 28.0; 24.5; 24.5; 28.0; 28.0; (Light 28.0); 31.5; 31.5; 31.5; 31.5; 28.0; 31.5; 31.5; 31.5; 31.5; 31.5; 35.0; 35.0.

No. 34. Interval 10 min. Temp. 18°–18.5° C. Illumination 31440 M. C. S.: 21.0; 21.0; 24.5; 17.5; 21.0; 21.0; 17.5; (Light 17.5); 17.5; 17.5; 21.0; 21.0; 21.0; 21.0; 17.5; 17.5; 21.0; 21.0; 24.5; 24.5.

No. 35. Interval 10 min. Temp. 16° C. Illumination 31440 M. C. S.: 28.0; 24.5; 24.5; 21.0; 24.5; 21.0; (Light 21.0); 21.0; 17.5; 17.5; 14.0; 14.0; 17.5; 21.0; 17.5; 21.0; 17.5.



TEXT FIG. 4. Graphs 31–41 show the result of the application of light to eleven root hairs of white mustard, illumination varying from 6780 M. C. S. to 3153600 M. C. S. Graphs 42–44 show the result of continuous application of light (938 M. C.) over a period of 2 hours to three root hairs of white mustard. For discussion see text.

No. 36. Interval 10 min. Temp. 16°–17° C. Illumination 563040 M. C. S.: 21.0; 24.5; 24.5; 24.5; 24.5; 21.0; (Light 24.5); 24.5; 24.5; 24.5; 24.5; 28.0; 24.5; 24.5; 24.5; 28.0; 28.0; 24.5; 21.0; 21.0; 24.5; 24.5; 24.5; 24.5.

No. 37. Interval 10 min. Temp. 16°–16.5° C. Illumination 563040 M. C. S.: 14.0; 14.0; 17.5; 14.0; 17.5; 17.5; (Light 14.0); 14.0; 17.5; 17.5; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 10.5; 14.0.

No. 38. Interval 10 min. Temp. 17° C. Illumination 563040 M. C. S.: 24.5; 24.5; 21.0; 24.5; 21.0; 21.0; (Light 24.5); 21.0; 24.5; 24.5; 24.5; 24.5; 24.5; 24.5; 24.5; 24.5; 24.5; 28.0; 24.5.

No. 39. Interval 10 min. Temp. 16°–19° C. Illumination 3153600 M. C. S.: 17.5; 17.5; 14.0; 17.5; 17.5; 17.5; (Light 21.0); 17.5; 17.5; 17.5; 21.0; 17.5; 21.0; 21.0; 17.5; 17.5; 19.3; 19.3; 17.5; 17.5; 17.5.

No. 40. Interval 10 min. Temp. 18.5°–21° C. Illumination 3153600 M. C. S.: 24.5; 24.5; 24.5; 24.5; 21.0; 24.5; (Light 28.0); 28.0; 24.5; 28.0; 28.0; 21.0; 24.5; 21.0; 21.0; 17.5; 24.5; 21.0; 21.0.

No. 41. Interval 10 min. Temp. 18° C. Illumination 3153600 M. C. S.: 21.0; 21.0; 21.0; 17.5; 21.0; 21.0; (Light 24.5); 24.5; 24.5; 24.5; 21.0; 24.5; 24.5; 24.5; 24.5; 24.5; 21.0; 24.5; 21.0.

No. 42. Interval 10 min. Temp. 18°–18.5° C. Illumination 938 M. C.: 31.5; 31.5; 28.0; 28.0; 31.5; 28.0; (Light 28.0; 31.5; 28.0; 31.5; 31.5; 31.5; 31.5; 35.0; 35.0; 31.5; 28.0; 28.0).

No. 43. Interval 10 min. Temp. 15.5°–17.5° C. Illumination 938 M. C.: 17.5; 14.0; 14.0; 14.0; 14.0; 14.0; 17.5; (Light 17.5; 17.5; 17.5; 17.5; 17.5; 17.5; 21.0; 17.5; 17.5; 17.5; 14.0; 14.0).

No. 44. Interval 10 min. Temp. 15°–16.5° C. Illumination 938 M. C.: 21.0; 17.5; 21.0; 17.5; 17.5; 17.5; (Light 21.0; 21.0; 17.5; 21.0; 24.5; 21.0; 21.0; 21.0; 21.0; 21.0; 21.0; 21.0; 17.5).

No. 31, illumination 6780 M. C. S., shows great uniformity of growth in light. No. 32 shows two decided intervals of retardation following light. That this is due to light may be questioned, as no such retardation is shown in the previous study or in those following.

No. 33, illumination 31440 M. C. S., shows little variation in growth after lighting. In general, the rate of growth is more rapid after the lighting period. No. 34 shows variations equaling 7 microns per period after light. Equal variations may be noted in the hour just preceding lighting, while the root hair was still in darkness. No. 35 shows a retardation to 14 microns per interval about 30 minutes after lighting. This is 7 microns per interval less than recorded in the dark. If it were not for the two preceding investigations which show no such retardation, it might be suspected of being a light-growth reaction.

No. 36, illumination 563040 M. C. S., shows much the same variations after lighting as while in darkness. There are two periods of more rapid growth following the application of light. Both nos. 37 and 38 show great uniformity of growth.

With an illumination of 3153600 M. C. S., trouble was encountered with increased temperature as in the case of *Raphanus sativus* under the same intensity. Swelling was very common, the root hairs in this case ceasing to elongate within a few minutes, making them useless for study. Con-

sequently three root hairs were chosen which did not swell at the tip during the application of light. Their rates of growth are given in lists nos. 39, 40, and 41. With the exception of no. 40, none show more retardation after lighting than in continuous darkness. The slight retardation in no. 40 appears 1½ hours after lighting and lasts but one interval.

Obtaining no positive results from short periods of lighting, continuous lighting was finally tried. An intensity of 938 M. C. was used. A light intensity greater than this could not be applied under the conditions, without increasing the temperature to an extent which would interfere with the experiment. By examining nos. 42, 43, and 44, it can be seen that in no case did the rate of growth after exposure drop below the growth rate in the dark. The oscillations following the application of light resemble closely the variations while grown in the dark.

In conclusion it may be said that *neither the root hairs of Raphanus sativus nor those of Sinapis alba show any reaction definitely attributable to light up to an intensity above 3153600 M. C. S., and Sinapis alba shows no such reaction in continuous lighting for two hours under an intensity of 938 M. C.*

It may be asked why the root hairs of *Sinapis alba* fail to show any light-growth reaction, while the root, as found by Blaauw (7), shows a decided retardation under light. An answer may be found by determining whether light influences cell-division or cell-elongation. Sachs (38) investigated certain algae (Spirogyra, Ulothrix, Hydrodictyon, and others) and concluded that cell-division takes place chiefly at night in these forms. He also states that in *Pilobolus crystallinus* the splitting of the protoplasm in the sporangium into spores takes place only at night, the spores being thrown out in the light. He concludes from these studies that light retards cell-division. Later investigations of this problem have not been convincing. Karsten (21, 22) studied carefully the rate of cell-division in light and darkness in roots, stems, and leaves, and also in algae. He examined his material at intervals to determine the proportion of dividing to resting cells. His results were not very conclusive. Friesner (15), probably the most recent careful investigator of this question of periodicity of cell-division, concludes that the times of maximum and minimum cell-division in a root are dependent upon the time of initiation of the metabolic processes, not upon alternating periods of light and darkness. Berinsohn (4), working with the roots of *Allium Cepa*, determined by sectioning the proportion of dividing to resting cells in roots grown in the light. He compared these results with those obtained from roots grown in the dark. He found a larger proportion of dividing cells in roots grown in the dark, and concluded that light has a retarding effect on cell-division. If light has such a retarding effect, we should have this factor entering and tending to decrease the rate of growth.

It may be pointed out that in the root there is a complex tissue composed of thousands of cells. Light may have a retarding effect on the elongation of

these cells which, multiplied many times as it would be in the root, could be easily measured. However, this retardation as expressed in an individual cell (as the root hair) may be too slight to be measured by the methods employed in this investigation, or it may be covered by fluctuating variations in the growth rate. The fact, however, that many of the root hairs investigated exhibited rather an increase than a decrease in their growth rate after light was applied, would lead one to question the retarding effect of light on cell-elongation.

There are several possible sources of error in an investigation such as this. It is impossible to read with absolute certainty the amount of root-hair elongation by the use of an eyepiece micrometer, because (1) the root hair may not be growing exactly at right angles to the line of vision; (2) the small size of the micrometer scale and root hair makes it impossible to be absolutely certain of the exact location of the root-hair tip; (3) it is impossible to read fractions of spaces on the micrometer scale with any degree of accuracy. It may be that, with the development of more delicate apparatus for measuring the growth of the cell, and with stronger light intensities than were used in the investigations here reported, a light-growth reaction may be discovered in root-hair cells. But from the evidence thus far obtained it must be held, for the present at least, that light has no effect upon the enlargement of root-hair cells.

The Effect of Temperature on the Rate of Root-hair Elongation

The first work of importance on the relation of temperature to the growth processes in higher plants is that of Sachs (37), who about 1860 studied the effect of temperature on germination. He measured the amount of growth of soaked seeds for a given period at a given temperature. Prior to the experiment the seeds were soaked usually for about 48 hours, the time being measured from the end of the soaking. Miss Leitch (27) points out the defects in this method, an important one being that there is great variation in the rate at which roots of the same species, and treated in the same manner, burst through their seed coats.

Koeppen (23) was the next important student of this problem. Working with a number of different seedlings, including maize, he obtained varying results. His curve for maize as well as those for many other plants shows two optima. Lehenbauer (26), one of the more recent investigators, using more refined methods found no indication of the double optimum. Other investigators, as Sachs (37) and Davenport (11), have described the curve for maize as having a single optimum. Lehenbauer from his work on maize concludes that the term "optimum temperature for growth" means little unless the time of exposure is definitely stated. He found with high temperatures (31° C. and above) a decrease in the growth rate with prolonged periods of exposure, while this did not occur with temperatures near the minimum (12°–14° C.). Miss Leitch (27) considers that the term

"optimum" should be used for the highest temperature at which growth takes place at a constant rate. She introduces the term "maximum-rate temperature" for the temperature at which growth reaches its highest intensity over a short period of time.

As regards the influence of a sudden change of temperature on growth, Askenasy (2) found this dependent on the position of the lower limit used. If the lower limit still permitted growth, a change to a higher temperature resulted in immediate increase in the growth rate. When, however, the minimum temperature used was near the zero point of growth for the plant studied, an increase in temperature was followed by a more or less tardy resumption of the normal growth rate. Pfeffer (35) noted similar results in some of his investigations. Godlewski (16) found in the case of the epicotyl of *Phaseolus vulgaris* that an exposure to sudden changes of temperature, either upward or downward, resulted in a temporary decrease in the growth rate. True (45), working with *Vicia faba*, found that a transfer of the radicle to a suddenly lowered temperature (near 0° C.) resulted not only in a checking of elongation but in actual contraction. Measurements at short intervals showed that this contraction lasted for five minutes. The root remained at a standstill for about one half hour, then began to elongate slowly and irregularly. Being brought back to normal temperature, the root returned to about two thirds its normal growth rate. Between the temperatures of 18° and 30° C. he did not consider that a change in temperature produced any very noticeable change in growth. There was some checking in the growth rate during the first 15 minutes, followed by an increased rate of elongation during the second 15 minutes. He considers this retardation a turgor change. Pfeffer (35) has found experimentally that the turgor pressure is influenced by temperature changes in the same manner as gas pressure.

The work on temperature in its relation to root hairs, as in the case of light, has been confined to studies of its effect on the presence or absence of hairs and on their abundance if present. Miss Snow found (44) that with high temperatures and sufficient moisture there was a tendency to decrease the number of root hairs produced in consequence of the increased ventral elongation of the cells of the root. Wollny (49) reported an increase in the number of hairs on aërial organs due to aërial transpiration. Here transpiration may affect hair-production through its influence on plant temperatures.

The purpose of the investigations described below was to determine if slight changes in temperature, between the limits of 17° and 27° C., would affect the rate of elongation of a root hair which had been growing at a constant temperature. These temperatures, while somewhat below the optimum given for most plants, still approach it and are removed some distance from the minimum.

As in the study of the effect of light on growth, roots of *Raphanus sativus*

and *Sinapis alba* were used. These were grown in the same manner as previously described, the investigations being carried on in the dark in the same constant-temperature room. A temperature chamber was devised which could be attached to the stage of the microscope (fig. 2, Pl. LXII), and the moist chamber containing the growing roots was placed in this. The thermometer was passed through an opening in the top of the temperature chamber, its bulb being inserted in a small vial surrounded by a layer of saturated filter paper. This imitated rather closely the existing conditions in the moist chamber. A small opening in the side of the temperature chamber, of the proper size to admit the objective of the microscope, enabled the observer to measure the growth rate of the root hairs by means of the eyepiece micrometer. The rate of growth was observed at 5- to 10-minute intervals for a half hour or more. For a cooling solution a bottle containing crushed ice was placed in the temperature chamber, care being taken not to disturb the mounted root hair. For a heating solution a bottle was partly filled with water and just before inserting it in the chamber 10 or more cc. of concentrated sulfuric acid were poured into this. The reaction produced developed heat sufficient to raise the temperature of the chamber $2\frac{1}{2}$ to 3 degrees C. and rarely even more, within 10 to 15 minutes.

Lists numbered 45–47 show the effect of the cooling solution on root-hair elongation in *Sinapis alba*. Readings were taken at 10-minute intervals in nos. 45 and 46, and at 5-minute intervals in no. 47. *Below each successive increment is given the temperature in italics.*

No. 45. 21.0; 17.5; 21.0; 17.5; 14.0; 14.0; 14.0; 14.0; (Cooling solution 7.0; 5.3; 1.8; 3.5;
17 17 17 17 17 17 17 17 (15.5 15.5 15.5 15.5
3.5; 7.0; 7.0; 7.0).
15.5 16 16 16)

No. 46. 28.0; 24.0; 28.0; 24.0; 28.0; 24.0; (Cooling solution 14.0; 10.5; —3.5; —3.5; —3.5;
18.5 18.5 18.5 18.5 18.5 18.5 (16.5 16 15.5 15.5 15.5
0.0; 7.0; 0.0; 3.5; 3.5; 0.0; 0.0).
16.5 17.5 17.5 18 18 18 18.5)

No. 47. 7.0; 10.5; 8.8; 8.8; 10.5; 10.5; 10.5; 10.5; 14.0; 10.5; 14.0; 10.5; (Cooling solution
18 18 18 18 18 18 18 18 18 18 18 18 (
7.0; 5.3; 1.8; 0.0; 0.0; 0.0; 0.0; 0.0).
16 15 15 15 16 16.5 17 18)

Lists numbered 48–51 show the effect of the cooling solution on root-hair elongation in *Raphanus sativus*. The interval in each case is 5 minutes.

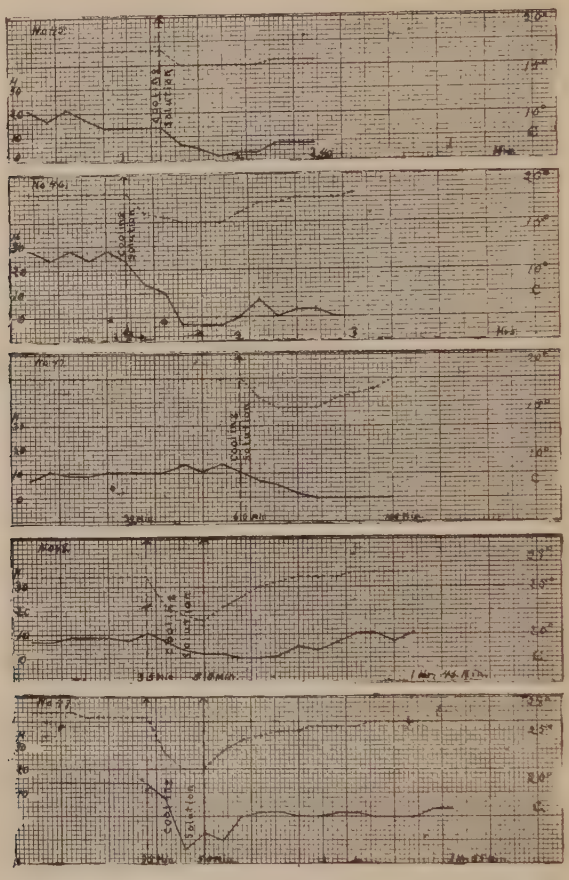
No. 48. 7.0; 7.0; 8.8; 8.8; 8.8; 7.0; 10.5; (Cooling solution 7.0; 3.5; 1.8); 1.8; 0.0; 0.0; 1.8;
26 26 26 26 26 26 26 (23 22 21.5) 23 24 25 25.5
5.6; 3.5; 7.0; 10.5; 10.5; 7.0; 10.5.
26 26 26 26.5 26.5 26.5 26.5

No. 49. 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; 14.0; (Cooling solution 7.0; 14.0; —7.0); —10.0;
27 27 27 26.5 26.5 26.5 26.5 (22.5 21 21) 23
0.0; 1.8; 1.8; 0.0; 0.0; 1.8; 1.8; 0.0; 0.0; 0.0; 3.5; 3.5.
24 24.5 25 25 25.5 25.5 25.5 26 26 26 26 26

No. 50. 14.0; 17.5; 14.0; 17.5; 17.5; 17.5; 14.0; (Cooling solution 7.0; 0.0; 0.0).
27 26.5 26.5 26.5 26.5 26 26 (25 24 24)

No. 51. 14.0; 14.0; 14.0; 17.5; 17.5; 17.5; 14.0; (Cooling solution 10.5; 10.5; 3.5; 0.0).
27 27 26.5 26.5 26.5 26.5 26.5 (25 25 25 25)

No. 52 shows the effect of the heating solution on a root hair of *Sinapis alba;* nos. 53 and 54 show the effect of a similar solution on root-hair elongation in *Raphanus sativus.* Interval 5 minutes in each.



TEXT FIG. 5. Numbers 45–47 show the effect of a cooling solution on the rate of root-hair elongation in white mustard. Nos. 48 and 49 show the effect of a similar solution on the elongation of root hairs of radish. The solid line gives the rate of root-hair elongation, the broken line the temperature.

No. 52. 21.0; 21.0; 24.5; 24.5; 21.0; 21.0; 21.0; 24.5; 24.5; 24.5; (Heating solution 17.5;
25 25 25 25 25 25 25 25 25 25 (27
38.5; 17.5; 7.0; 0.0; 0.0).
30 32.5 32 32 32)

No. 53. 10.5; 14.0; 10.5; 14.0; 14.0; 10.5; 10.5; (Heating solution 7.0; 17.5; 14.0; 14.0;
25 25 25 25 25 25 25 (26 26.5 26.5 27
10.5; 17.5; 17.5).
27.5 27.5 28)

No. 54. 14.0; 17.5; 17.5; 17.5; 17.5; 14.0; (Heating solution 21.0; 28.0; 21.0); 14.0; 14.0;
26 26 26.5 26 26 26 (27.5 28.5 29) 28.5 27.5
14.0; 14.0; 17.5; 14.0; 14.0; (Heating solution 21.0; 24.5; 17.5); 10.5; 10.5; 14.0; 14.0;
27 27 27 26.5 26.5 (27.5 28.5 29) 28 27.5 27 27
14.0; 17.5; 17.5; 17.5; 17.5.
26.5 26.5 26.5 26.5 26.5

No. 45 shows during the first 10 minutes after a drop of 1.5° C. a retardation of elongation to one half of its former rate, that is, from 14 to 7 microns. After 20 minutes more, the temperature remaining constant, the rate of growth dropped to 1.8 microns per interval. It increased during the next two intervals to 3.5 microns, and at the end of one hour was again 7 microns per interval, which rate was maintained for at least 20 minutes longer.

No. 46, with a cooling of two degrees (18.5°–16.5° C.), shows a reduction in the growth rate of 10 microns (24 to 14 microns) during the first 10 minutes. At the end of 30 minutes, with a temperature of 15.5° C., a shortening of the root hair was noted. This amounted to 3.5 microns for the 10-minute interval, and was continued through three intervals at the same rate. Movement then ceased, and later, with an increase in temperature, some elongation was again noted. However, this was little more than sufficient to bring the root hair back to its length before contraction began.

No. 47 shows a reduction in the growth rate from 10.5 microns to 7 microns per interval during the first 5 minutes after a cooling of two degrees (18° to 16° C.). The rate then decreased gradually with a drop of one degree, and at the end of 20 minutes, at 15° C., growth had ceased and was not resumed during the period of observation. No contraction was noted.

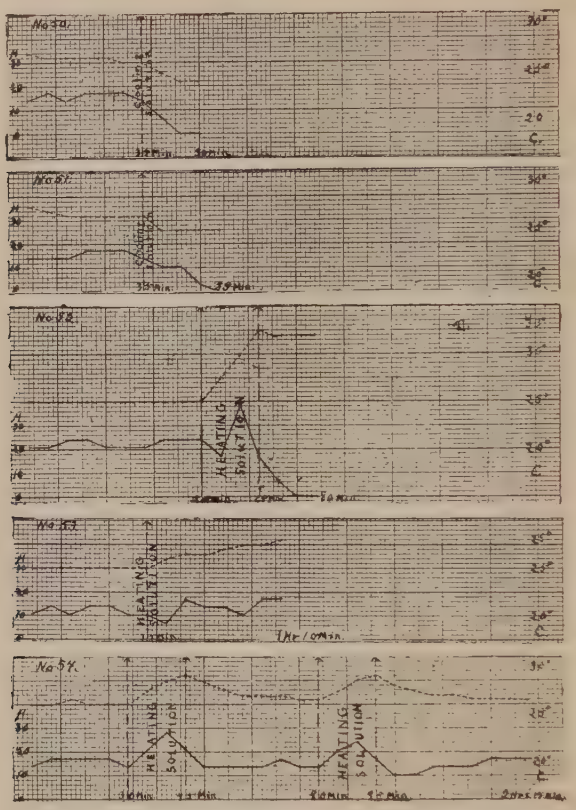
No. 48 shows the results of applying the cooling solution during 15 minutes. In this time the temperature was gradually reduced from 26° to 21.5° C. At the same time we find a gradual reduction in the growth rate from 10.5 microns per interval just before cooling to 1.8 microns at the time the cooling solution was removed. Although the temperature rose during the next 10 minutes $2\frac{1}{2}$ degrees (from 21.5° to 24° C.), the rate of growth continued to decrease, and finally growth ceased for a period of 10 minutes. It was then slowly resumed at a temperature of 25.5°, and 15 minutes later had returned to normal.

No. 49 shows a decided contraction of the root hair with a decrease in temperature of $5\frac{1}{2}$ degrees (from 26.5° to 21°). Later, elongation was resumed intermittently, but with a return to normal room temperature the growth was extremely slow.

Nos. 50 and 51 show a reduction in the growth rate to zero in from 10 to 20 minutes, with a temperature reduction of only $1\frac{1}{2}$ to 2 degrees.

No. 52 shows the effect of an increase of temperature from 25° to 32.5° C. The growth rate was first retarded and then increased 14 microns over that before heating. However, at a continuous temperature of 32°, the root hair became swollen at the tip and no further growth was noted.

No. 53 shows a less decided reaction with an increase in temperature from 25° to 26° C. There was first a retardation and then an acceleration in growth. The acceleration here was slight, and growth soon returned to that found before heating. As the temperature increased to 28°, a second acceleration was noted.



TEXT FIG. 6. Nos. 50 and 51 show the effect of a cooling solution on root hairs of radish. No. 52 shows the effect of a heating solution on a root hair of white mustard; Nos. 53 and 54 show the effect of a similar solution on root hairs of radish. For discussion see text.

No. 54 shows an acceleration in growth with an increase in temperature of 3° C. Two applications of heat were made, the growth rate increasing in both cases during heating and dropping to normal shortly after heat was removed. The return of the growth rate to that found before heating took place more rapidly than the drop of temperature. No swelling was noted in this hair.

These investigations indicate that the root hair is extremely sensitive to changes of temperature when grown within the limits of 17° to 27° C. A drop in temperature taking place within a period of 5 to 15 minutes results in

a decrease in the growth rate. In some cases recovery is partial or even entire. In other cases elongation ceases and is not resumed. A reduction in temperature of 5 to 6 degrees results in a contraction of the root hair. With a reduction of one to two degrees no shortening is noted, although elongation may be entirely stopped. This shortening may be the result of a turgor change within the root-hair cell.

A gradual increase in temperature of $2\frac{1}{2}$ to 3 degrees results in a temporary acceleration of growth, which, however, soon returns to normal. This return to normal rate may take place more rapidly than the return to room temperature. An increase in temperature of from 3 to 6 degrees results in swelling of the root-hair tip and cessation of growth. In some cases growth may be resumed later. It was previously noted that growth under high light intensities, where the temperature factor could not be entirely eliminated, resulted in such a swelling as described.

The work of previous investigators has been with multicellular organs (mostly the radicles or young shoots of seedlings) over one or more days with readings in most cases one half to three hours apart. Their variations in temperature have also been much greater than those used in the present investigations. They failed to find any marked effect on growth in consequence of such slight temperature changes as produced a decided reaction in the root hair. This failure may be due, in part at least, to the fact that the cells making up complex tissues are more protected from sudden changes of temperature. Thus, in the root, the epidermal cells and those of the outer cortical region protect the internal cells from sudden changes of temperature. On the other hand, the long slender root hair (exclusive of the basal portion of the epidermal cell from which it arises) is directly exposed on all sides to the varying temperature changes of the surrounding atmosphere. In spite of this difference there is some similarity in results. Thus, Godlewski (16) and True (45) found that a lowering of temperature resulted in a temporary reduction in the growth rate. True, in the case of *Vicia faba* already mentioned, found, when the radicle was subjected to suddenly lowered temperature, that not only a cessation of growth but actual contraction followed. He used very low temperatures, however (0° C.), and found little effect of temperatures from 18° to 30° C. Askenasy (2) found that an increase in temperature, when the root was grown near the optimum, resulted in an increase in the growth rate.

The effect of temperature on the elongation of the root hair may be an effect either on the nature of the plasma membrane, on the osmotic pressure or colloidal imbibition of the cell contents, or on the extension of the cell wall. Livingston (30) states that a potent cause for great increase in protoplasmic permeability in some instances is a lowering of temperature. Thus, if a filament of a common alga is carefully dried and placed in olive oil, whose temperature is then rapidly lowered, a film of water may be seen to form about the filament and partial plasmolysis may be observed.

When the temperature is again brought back to normal, the extruded water is absorbed. Greely (17) has shown that complete plasmolysis can be produced in Spirogyra by lowered temperature.

The increase in cell permeability due to lowered temperature may account for the decrease in elongation in certain of the root hairs studied. Partial plasmolysis in the root hairs would doubtless result in the cessation of elongation and even in contraction. The growing root hair being under tension, a stoppage of the growth processes with lowered osmotic pressure would, if sufficiently marked, result in a contraction and shortening of the wall due to its elasticity.

Krabbe (24), experimenting upon the effect of a rise in temperature upon the absorption of water by various plant cells, found the rate of absorption to rise with the temperature. Ursprung (46) found with shoots of Fagus and Thuja that an increase in the temperature of the water in which the shoots were immersed was followed at first by no increase in the water-absorption. Later there was a sudden increase in absorption, and finally a decrease to the zero point. Van Rysselberghe (47) and Brown and Worley are others who have worked on the relation of temperature to the permeability of protoplasm and the ability of tissues to absorb water.

The effect of changes of temperature on the osmotic pressure of various colloids has been studied with varied results. Moore and Roaf (32) found that the osmotic pressure of gelatin solutions increases faster than the absolute temperature. Recently, C. R. Smith (43) has studied the variations in osmotic pressure of gelatin in water. He concludes that "the swelling of gelatin is the result of osmotic pressure within the jelly, with the jelly acting as an imperfectly resisting membrane, the more so when highly swollen." This indicates that the effect of temperature upon the osmotic pressure of the cell may be practically identical with its effect upon colloidal imbibition. Shull and Shull (41) have found that gelatin absorbs water for a long period from a saturated atmosphere—in fact for a much longer period (47 days) than these root hairs continued to absorb water. It may be, therefore, that the whole process of root-hair elongation is primarily a matter of colloidal imbibition, with osmotic pressure and cell-wall deposition as secondary. Lillie (29) noted interesting thermal after-effects, or so-called hysteresis phenomena, in gelatin solutions. These, when heated and afterward cooled, continued for some time to show a higher osmotic pressure than when kept continuously at the lower temperature.

Further evidence of the importance of the effect of temperature on colloidal imbibition in connection with the growth of these root hairs is shown by the swelling of their tips with sudden changes in temperature. This swelling must involve a change in the cell wall as well as in the interior of the cell. Recent evidence indicates that the cell wall is colloidal in nature, and the swelling of the root hair above described contributes to the support of this idea.

Summary

1. The grand period of elongation of the root hair resembles the grand period of growth in plant tissues in general, except that the middle of the curve is more extensively flattened in the case of the root hair. There is a gradual increase in the growth rate during the early part of the period and a gradual diminution in rate at the close.

2. There is little difference in the growth rate of root hairs on any one root. Slight differences in length of root hairs in any one region are due more to age than to rate of growth.

3. There appears to be a definite relation between number of root hairs and rate of growth. On species having many root hairs, the hairs elongate more slowly than on those with fewer hairs.

4. There is a definite relation between root-hair elongation and lateral movement, the rate of elongation being gradually accelerated as the lateral movement of the hair is retarded. Apparently cellular interaction is a factor here. The checking of cell-elongation in the epidermis due to a decrease in the rate of growth in the adjacent cortical cells results in an evagination in certain epidermal cells which develop root hairs.

5. Root hairs of *Raphanus sativus* and *Sinapis alba* show no noticeable light-growth reaction in light intensities up to 3153600 M. C. S., and the latter species shows no such reaction in continuous lighting for two hours under an intensity of 938 M. C. It is therefore suggested that the light-growth reaction in multicellular organs is not due to a change in the rate of cell-elongation, but to some other effect of light, such as a change in the rate of cell-division.

6. Root hairs of *Raphanus sativus* and *Sinapis alba* grown at a constant temperature within the limits of 17° and 27° C., show a decided reaction to changes of temperature of from one to six degrees brought about within a period of from 5 to 15 minutes. A drop in temperature results in a decrease in the growth rate and sometimes even in contraction of the root hair with no indication of swelling. In some cases recovery of the growth rate is partial or even entire; in other cases elongation ceases and is not resumed. A rise in temperature of $2\frac{1}{2}$ to 3 degrees in the time given above results in a temporary increase in the growth rate, which soon returns to that before heating. The return to what we may call the normal rate often takes place while the temperature of the surrounding air is still above normal. These results indicate that a change in temperature affects the rate of growth in multicellular organisms by modifying the rate of cell-elongation.

7. It is concluded that the effect of temperature upon the rate of growth of tissues is in part at least an effect upon the osmotic pressure and imbibition of the cell colloids, rather than simply an effect upon the rate of chemical reactions within the tissues.

This study was carried out in the laboratory of plant physiology at the University of Iowa, and the writer wishes to express his appreciation to

Dr. C. H. Farr, who suggested the problem, and whose constant interest and helpful suggestions have been invaluable aids in the completion of the experiments.

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EXPLANATION OF PLATE LXII

FIG. 1. Moist chamber containing radish seedlings.

FIG. 2. Temperature chamber used in investigating the effect of varying temperatures on the rate of root-hair elongation.

FIG. 3. Photograph showing swelling of root hairs due to increased temperature. These hairs continued to elongate after swelling.

FIG. 4. Border of radish root in the root-hair zone. Photographed at 15-minute intervals (right to left). Note the lateral (downward) movement of the young root hairs shown in the lower portion of the photograph.

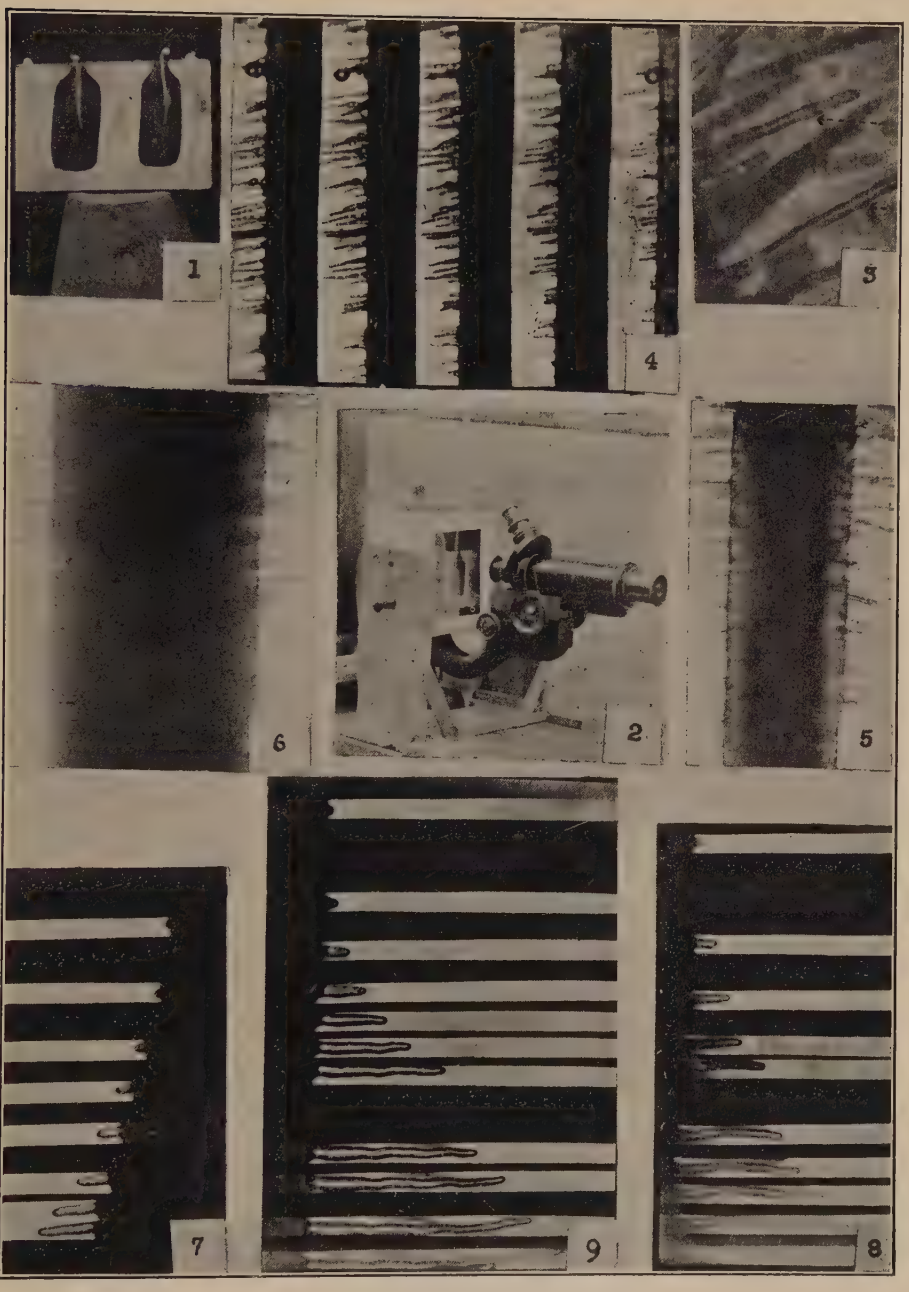
FIG. 5. Photograph of radish root in the root-hair zone.

FIG. 6. Photograph of pop-corn root in the root-hair zone.

FIG. 7. Root hair of pop corn photographed at 15-minute intervals for one hour and forty-five minutes. Spaces between the photographs show the amount of lateral (downward) movement during each interval. Note the decrease in the rate of root-elongation with the increased lengthening of the root hair.

FIG. 8. Root hair of pop corn photographed at 15-minute intervals. Spaces between the upper five photographs show lateral movement. The lower five show root-hair elongation only.

FIG. 9. Root hair of radish photographed at 15-minute intervals for $2\frac{1}{2}$ hours. The spaces between the upper seven photographs show the amount of lateral movement during each interval. The lower four photographs show root-hair elongation only.



JEFFS: ELONGATION OF ROOT HAIRS